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PAIR BOND MAINTENANCE IN PILEATED WOODPECKERS AT ROOST SITES DURING AUTUMN

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ABSTRACT.—Individuals in a number of bird species have the opportunity to maintain contact with their mates during nonbreeding periods. This contact may be important to synchronize the partners' reproductive cycles before breeding begins. As a first step toward exploring the function of pair bond maintenance in nonbreeding birds, I studied the behavior of three pairs of Pileated Woodpeckers (*Dryocopus pileatus*) and an unpaired male at roost sites during autumn. At dawn and dusk, paired individuals exchanged visual, vocal, and other acoustical signals identical to those given during the breeding season. Demonstration tapping away from a nest is reported here for the first time. The possible function of these behaviors may be related to monitoring the partner's condition and investing in the pair bond to enhance future reproductive success. *Received 19 September 2002, accepted 01 March 2003.*

The pair bond of many birds is formed each spring as courting birds establish a relationship with their future mate. Once the nesting season ends, many birds cease to maintain the pair bond. However, in a diverse group of species, formation of a pair bond may occur long before spring, and termination of the pair bond at the end of reproduction may not occur (reviews in Oring 1982, Fowler 1995, Black 1996). Future and/or former mates may interact and cooperate with one another on a continuing basis throughout the year, or at least during part of the nonbreeding season. The investment into this relationship by individuals is referred to here as pair bond maintenance.

Advantages of pair bond maintenance outside the breeding season are unclear and poorly documented. Some hypotheses suggest that individuals gain reproductive benefits from spending time with a partner prior to breeding. For instance, pair members familiar with each other may achieve reproductive synchrony earlier or to a greater degree compared to other pairs (Butterfield 1970, Rowley 1983, Ens et al. 1996). Other hypotheses depict the mate as a resource that must be protected, nurtured, and retained in order to avoid high costs that might be involved with the loss of a partner through death or divorce (Ens et al. 1993, Choudhury 1995, Hogstad 1995). These hypotheses are hard to evaluate since in many cases it is not clear which behaviors are involved with pair bond maintenance and how the behaviors might be experimentally manipulated without altering social or environmental conditions. Because different species have various natural histories, the behavioral mechanisms by which pair members of each species can protect, nurture, and gain familiarity with each other differ. Thus an important first step in addressing questions about pair bond maintenance during the nonbreeding season is to document the frequency and context of behaviors that may facilitate pair bond maintenance.

Pileated Woodpeckers (*Dryocopus pileatus*) are thought to pair with the same mate in successive reproductive seasons. Some of these pairs maintain contact with each other during winter while others do not (Bull and Jackson 1995). The nature of this nonbreeding season contact is not well described. However, Pileated Woodpeckers give loud "wuk" vocalizations near their roost sites (Bull and Jackson 1995), and these may help the pair maintain contact with each other (Kilham 1974). "Wuk" calls may be exchanged between pair members in the manner of a duet (Short 1982). Other behaviors, such as head swinging, demonstration tapping, and exchanges of various vocal signals, have been documented as part of courtship (Kilham 1959, 1979).

Because Pileated Woodpeckers usually are found at low densities, and parental investment is substantial and nearly equal between males and females (Short 1982, Bull and Jackson 1995), it seems likely that losing a mate

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through death or divorce would be costly. Thus, monitoring the current mate's condition, even during nonbreeding periods, may be an important investment in future reproductive success. It is in this framework that I discuss behavioral signals observed at roost sites during autumn. I also present data on the characteristics of male and female roost cavities and the timing of roost entry in relation to weather conditions. Both types of data could potentially affect pair interactions.

METHODS

I searched for roost sites of Pileated Woodpeckers in the mixed forests of Acadia National Park, Maine (44° 26′ N, 68° 21′ W), between 12 September and 20 November 1995. Canopy species included red oak (*Quercus rubra*), white birch (*Betula papyrifera*), American beech (*Fagus grandifolia*), and red spruce (*Picea rubens*). Roosting areas (but not the cavities themselves) were relatively easy to find because past wildfires in my study area created a patchy landscape of large-diameter trees where burn intensity was low. Once a roost cavity was found, I observed each individual's behavior during the evening and morning from a position ≥20 m from the tree where each roost hole was located. I used the same observation points each time, and the roosting birds seemed to ignore me. Evening behavioral observations began 90 min before sunset and ended 10 min after roost entry. Morning observations began 30 min before sunrise and ended 10 min after an individual left the roosting area.

I collected data on selected weather variables to determine whether variation in roosting time was related to cloud cover, air temperature, or barometric pressure. Cloud cover was recorded as the percentage of sky obscured at the time of roost entry: clear (0–34%), partly cloudy (35–69%), and cloudy (70–100%). I obtained temperature and barometric pressure readings from a weather station located on the College of the Atlantic campus, 11.6 km from the farthest roosting site. I used ANOVA (SAS Institute, Inc. 1999) to determine whether the timing of roost entry was related to one or more of the weather variables. Because my sample size was too small to employ a repeated measures test, I analyzed each individual's data separately.

During evening observations, I noted acoustical signals, including vocalizations and drumming, and head swinging displays that occurred ≤3 min of roost entry. I chose this time interval because the location of individuals (and thus the identity of those giving signals) was not always known before woodpeckers arrived at the roost tree. During morning observations, I collected behavioral data on individuals for up to 30 min, depending upon how quickly they left the roost area.

RESULTS

I studied eight unmarked individuals, including three male-female pairs (Campus, Point, and Nubble) and two males (Lake and Head) that apparently had no female partners. Five of eight individuals used multiple roost sites, and the number of observations for each individual varied according to how rapidly I could locate the next roost. I identified individuals by sex and location of roosts. Trees with roost cavities usually were clumped, and the data reported here are based on the five patches occupied by the pairs and single males; low coastal mountains separated each patch. I have no evidence that more than two individuals ever frequented the same patch. The maximum distance between known roost cavities within a patch was 350 m, and the minimum distance between the patches I studied was 2.5 km.

The single roosts of one male-female pair (Campus pair) were only 35 m apart and could be monitored concurrently from the same observation point. Other paired individuals roosted 55–135 m from their mate when both roost locations were known.

I found few differences between male and female roost trees. Male and female roosts were in similar species, at similar heights from the ground, and in a mix of live and dead trees (Table 1). However, males appeared to use newer roost cavities than did females. The Campus male's roost was used as a nest during the previous spring, while the Campus female's roost was a nest three springs before (unpubl. data). The two roost cavities used by the Nubble male were excavated within the year, but the Nubble female's roost appeared older. I could not determine the age of the Point woodpeckers' roosts, but the roost cavities of the female had several more entrance

TABLE 1. Characteristics of cavity trees located near Pileated Woodpecker roosting areas during autumn in Maine, 1995.

Location	Cavity occupant	Dates used	Tree species	Tree condition	# entrances	Height of lowest entrance (m)	dbh (cm)
Campus	Male	18 Sept to 20 Nov	Norway maple (*Acer platanoides*)	Live	1	9	42
	Female	25 Sept to 20 Nov	Norway maple	Dead	1	7	45
Point	Male	12 Sept to 30 Oct	Gray birch (*Betula populifolia*)	Dead	2	8	58
	Male	20 Nov	Red maple (*A. rubrum*)	Live	1	16	40
	Female	28 Sept to 5 Oct	Gray birch	Dead	3	7	40
	Female	31 Oct to 4 Nov	Gray birch	Live	5	18	43
	Not used		Gray birch	Dead	1	8	39
	Not used		Gray birch	Dead	1	9	28
	Not used		Red spruce (*Picea rubens*)	Dead	1	15	37
Nubble	Male	21 Oct to 23 Oct	Beech (*Fagus grandifolia*)	Live	1	2	44
	Male	24 Oct to 5 Nov	Beech	Live	1	6	51
	Female	21 Oct to 23 Oct	Red maple	Dead	1	20	53
	Not used		Red maple	Dead	2	15	44
Lake	Male	10 Oct to 19 Nov	Red maple	Dead	2	8	66
	Not used		Red maple	Dead	1	8	40
Head	Male	4 Oct to 9 Oct	Beech	Live	2	5	47
	Not used		Red Oak (*Quercus rubra*)	Live	1	3	42

holes than the male's cavities (Table 1), which could indicate that the ages of her cavities were older than those used by the male. All three pairs excavated new nests within 25 m of a known roost cavity during the spring following my study.

Evening roost entry.—Vocalizations recorded during the 3 min prior to roost entry consisted mostly of "wuk" calls, often combined during a continuous bout of sound lasting 5 s or more. I frequently heard these calls throughout the afternoon as well. The Campus male and female gave "wok" calls, considered a courtship call by Kilham (1959). This pair also gave head swinging displays while on the roost tree, and all paired individuals gave drums or a short distance acoustical signal known as demonstration tapping (Table 2; see Short 1982 for descriptions of these signals). Bouts of tapping took place on the roost tree, sometimes from inside the roost itself. Other instances of tapping involved a series of 2–6 irregularly spaced taps, given on or near the roost tree.

I monitored the roost entry times of the Campus pair on 20 evenings during my eight-week study and found that the female entered her roost 0–47 min before the male (Fig. 1). It is not known what factors contributed to the campus female's decision to roost. Cloud cover, temperature, and barometric pressure together did not explain a significant amount of variation in her roosting time ($F_{4,19} = 0.66$, $P = 0.63$). However, the timing of the Campus male's roost in relation to his mate's roost time was related to cloud cover ($F_{2,19} = 6.88$, $P = 0.007$). This male entered his roost on cloudy days a mean of 11 min ± 4 SE after the female ($n = 7$), but roosted much later on clear days (32 min ± 5 SE after the female, $n = 9$; post-hoc comparison $t = 3.70$, df = 14, $P = 0.002$). The male's activities on clear days following the female's roosting time took place away from the roosting area, so the reason for his delay was unknown.

In contrast to the uncoordinated movements of the pair on clear evenings, the Campus pair arrived at the roost site together on six of seven cloudy evenings. When the female entered her roost, she looked in the direction of the male as he foraged nearby. Twice the male followed the female to her roost cavity's entrance, and spent several minutes preening there before flying to his own roost for the night. A similar situation was observed between the Nubble pair, except that it was the female who spent time at the opening of the male's roost after he had entered.

Morning roost exit.—All Pileated Woodpeckers occasionally removed sawdust, wood chips, fecal material, or feathers from roost cavities before exiting in the morning at sunrise. Woodpeckers frequently gave "wuk" calls and drums at that time (Table 2). Mates regularly responded to these signals with a similar bout of drumming, vocalization, or demonstration tapping. No published account of Pileated Woodpecker behavior has described demonstration tapping during the nonbreeding period. Below, I describe two of the most extended pair interactions that featured tapping.

On the morning of 4 October 1995, before the Campus female left her cavity, the male flew to near her roost, vocalized, and tapped. The female watched him for 14 min and then spent 6 min removing at least 45 bill-fulls of sawdust from her cavity. She exited her cavity, flew to the male's position, and demonstration tapped three times. The male drummed. She re-entered her cavity and tapped six times from inside. The pair exchanged signals in this manner for another 5 min, then the female flew from the area. The male remained, entered the female's roost cavity, and pecked at the cavity entrance and below the inside sill for 4 min. He then left the cavity and flew in the same direction that the female had gone. He returned, alone, to the female's roost tree 17 min later. He drummed on the outside and re-entered her cavity for 3 min. He gave a string of "wuk" calls on his way out of the cavity, and left the area again.

On the morning of 19 October 1995, the Campus male and female interacted at the

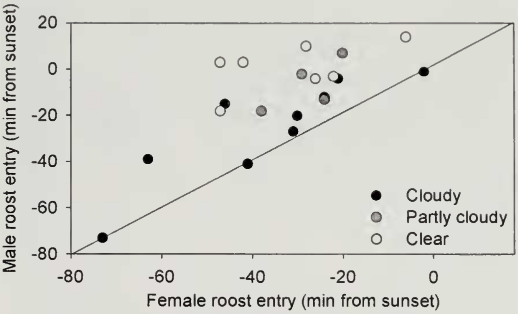

FIG. 1. The female Pileated Woodpecker of the "Campus" pair usually entered her roost before the male entered his, and she preceded the male by the most amount of time on clear evenings. Negative values are minutes before local sunset. Both birds enter their roosts concurrently along the diagonal reference line. Data are from Acadia National Park, Maine, autumn 1995.

male's roost cavity. The male initiated the activity by drumming near his roost tree. The female, who had not yet left her roost cavity, responded with a drum. She then left her roost and flew to the entrance of his roost. The male flew to her position, entered his cavity, and tapped from inside. The female reciprocated with more demonstration tapping. Both birds left the area together.

The timing of pair member interactions after sunrise depended upon when the individuals left their cavities. The Campus male left his roost a mean of 19 min ± 14 SD (n = 7) before the female. However, the Campus female was awake for a time before she left the roost, as I saw her look out from her cavity a mean of 17 min ± 15 SD (n = 7) before her roost exit. As in the above examples, she spent much of this time in the roost watching her mate and responding to his signals. After both birds had exited their respective roost cavities, the Campus male and female usually left the area together, and limited observations of the other two pairs also suggest that pair members rendezvoused with each other and interacted after leaving their roosts. For example, the Point male always (n = 7) flew in the same direction after leaving his roost, and two vocalizing or drumming Pileated Woodpeckers always were heard within a few minutes of his departure, from the same direction as his departure.

TABLE 2. Signals given by Pileated Woodpeckers at roosts in the evening (roost entry) and morning (roost exit). Values are mean signals/min ± SD and represent the short periods of time when woodpeckers were within 50 m of the roost cavity. Reciprocated signals are those which immediately followed a signal from the mate. Data are from Acadia National Park, Maine, autumn 1995.

	Entry or exit	Campus male $n = 29$ $n = 15$	Campus female $n = 20$ $n = 10$	Point male $n = 12$ $n = 7$	Point female $n = 6$ $n = 7$	Nubble male $n = 5$ $n = 2$	Lake male $n = 7$ $n = 5$
"Wuk" calls	entry	1.47 ± 1.35	0.90 ± 0.33	1.68 ± 1.68	0.84 ± 0.99	0.21 ± 0.45	0.42 ± 0.78
	exit	1.14 ± 0.93	0.27 ± 0.30	1.29 ± 0.48	1.05 ± 1.11	0	0.18 ± 0.42
"Wok" calls	entry	0.15 ± 0.36	0.27 ± 0.45	0	0	0	0
Head-swing bouts	entry	0.18 ± 0.39	0.06 ± 0.24	0	0	0	0
Drumming bouts	entry	0.06 ± 0.36	0.06 ± 0.24	0.09 ± 0.30	0	0.21 ± 0.45	0
	exit	0.60 ± 0.66	0.09 ± 0.30	0.90 ± 1.05	0.27 ± 0.69	1.35 ± 0.63	0
Tapping bouts	entry	0.03 ± 0.18	0.06 ± 0.24	0.18 ± 0.39	0.33 ± 0.51	0	0
	exit	0.18 ± 0.39	0.18 ± 0.39	0	0	0	0
Reciprocated signals	entry	14% of 50	21% of 24	22% of 23	43% of 7	0% of 2	0% of 3
	exit	21% of 32	17% of 6	29% of 17	60% of 10	66% of 3	0% of 1
<10 m association[a]	entry	14%	20%	27%	33%	20%	0%
	exit	20%	30%	14%	14%	0%	0%

[a] Percentage of observations during which mates came within 10 m of one another.

DISCUSSION

I observed Pileated Woodpecker pair members roosting 35–135 m from one another. Other studies confirm that short distances between pair member roosts are common (Hoyt 1957, Short 1982, Bull et al. 1992). It seems likely that pair bond maintenance is facilitated by the proximity of roost sites, since pair members can have greater potential for interaction. Even if roosts are not close, my observations and those of Kilham (1959) suggest that many pairs rendezvous in the morning after roost exit and in the evening before roost entry. Morning and/or evening interactions between mates also have been observed in other species, e.g., Wood Nuthatches (*Sitta europaea*; Radford 1954) and Carolina Chickadees (*Poecile carolinensis*; Pitts 1976).

Mate investment.—Rendezvous and spatial proximity during the day may benefit pair members in a number of ways. Breeding season reproductive benefits might accumulate with long term mate association; shorter term benefits such as mate protection and investment are also likely involved (Kilham 1976). The Campus female always exited in the morning after she saw the male leave his roost, and both Campus and Point females usually roosted earlier in the evening than their partners. Because males of other species protect their mates from predators (McKinney 1985, Hogstad 1995, Hannon and Martin 1996), it is possible that the male woodpeckers were acting as sentries during female roost entry and exit. Predation risk may be relatively high in Pileated Woodpeckers compared to other species (Kilham 1976, Bull et al. 1992). Adult predators include several hawks, owls, martens, and other mammals. Many of these are active at dawn and dusk and are known to lurk near roost cavities (Bull and Jackson 1995). The fact that the Campus pair coordinated roosting times more closely under cloudy conditions might suggest that visibility was lower (Bull 1978), and as a result, predation risk might have been higher on those evenings. In two of my study pairs, males seemed to play the role of sentry, but that does not exclude the possibility of female sentry behavior. For example, one night the Nubble female accompanied the male to his roost before she flew to her own.

Signaling and reciprocation.—Individuals frequently gave vocal and other acoustical signals near roost sites, and these included the "wuk" call and demonstration tapping. Both signals occasionally were repeated back and forth between pair members in the manner of a duet. One explanation for duets and other reciprocated vocal signals between mates during nonbreeding periods is that the signals indicate to nonmates that the territory is occupied by a mated pair and there is little chance that either a mate or the territory may be usurped by an intruder (Hall 2000). However, the tapping signals exchanged by mates were quiet and likely could not be heard by other conspecifics.

A different explanation is more likely. Many investigators regard sexual signals given during the nonbreeding season as part of pair bond formation or maintenance (Butterfield 1970, McKinney 1985, Choudhury and Black 1993). The assemblage of signals I observed during autumn is nearly the same as that exhibited by courting Pileated Woodpeckers during spring, lacking only the crest raising and wing spreading displays (Bull and Jackson 1995). Under the mate familiarity hypothesis, sexual signals given during the nonbreeding season may function to ensure continued familiarity between partners (Ens et al. 1996). This familiarity may improve reproductive success if repeated interaction between partners during the nonbreeding season results in better synchronization of reproductive or hormonal cycles (Hirschenhauser et al. 1999). In the present study, demonstration tapping is a good candidate for having a pair bond function. Woodpeckers regularly exchange taps at nest cavities (Kilham 1979), and it is interesting that the tapping I observed took place only within or immediately adjacent to trees that were past or future nest sites. Tapping thus seems closely tied to reproduction and may play a role in strengthening physiological and social relationships between mates.

At the same time, male-female association during fall (and winter) may aid an individual's effort to assess the quality of its mate. The mate investment hypothesis suggests that the mate is a resource that must be protected, nurtured, and retained in order to prevent its loss (Ekman 1990, Hogstad 1995). If true, pair members may monitor their partner regularly to assess whether the partner's relative quality has changed from the previous day. A partner that does not reciprocate a signal in the expected manner might be in poor health or may not be hormonally synchronized with the signaler. The signaling pair member may respond by changing the nature or intensity of its pair bond maintenance behavior (Hausberger and Black 1990, Hall 2000).

Clearly, more study is needed on Pileated Woodpeckers and other species with long term pair bonds. Brief roost site interactions at dusk and dawn may contribute significantly to pair bond maintenance, even in pairs that do not appear to interact during the rest of the day. Nonbreeding pair bond maintenance of any kind could have significant effects on survivorship and future reproductive success.

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